Distribution and nutrient limitation of surfgrass, *Phyllospadix scouleri* and *Phyllospadix torreyi*, Along the Pacific Coast of Baja California (México)

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Abstract

Three field surveys and an extensive review of surfgrass (*Phyllospadix*) specimens from herbarium collections in USA and Mexico were performed to delimit the geographical distribution of *Phyllospadix scouleri* and *Phyllospadix torreyi* along the coasts of Baja California (Mexico) which showed that both species had the same distribution in the peninsula with a southern limit at 24º 31' N. Cover estimates along 3 – 8 transects laid in the lower intertidal and upper subtidal of three locations in Baja California indicated that *P. scouleri* occurs shallower than *P. torreyi* when coexisting. A preliminary, short-term experimental increase of nutrient availability in the water column at one of the study sites suggested that the biomass and growth rates of *P. torreyi* were more limited by the availability of nutrients than those of *P. scouleri*.

Keywords: geographical range, depth distribution, nutrient limitation, seagrass, *Phyllospadix* spp., Mexico

1. Introduction

Surfgrasses (*Phyllospadix* spp.) rank among the few seagrass species able to grow on rocky substrate (Hemminga and Duarte, 2000) and to thrive under high wave exposure. These capacities render *Phyllospadix* species as the dominant seagrasses on the Pacific coast of North America (Cooper and McRoy, 1988; Kuo et al., 1988; Barnabas, 1994). Surfgrass is present in the subtidal and lower intertidal (Den Hartog, 1970; Phillips, 1979; Ramírez-García et al., 1998), and the rocky shore landscape is often formed by a mosaic including macroalgae, mussel beds, rocky outcrops, and tiny sand patches. Three species have been described along the Pacific coast of North America: *Phyllospadix torreyi* S. Watson, *Phyllospadix scouleri* Hooker, and *Phyllospadix serrulatus* Rupr. ex Ascherson (Den Hartog, 1970). *P. serrulatus* has a more northern distribution (from Alaska to Oregon) than the other two species, which extend from British Columbia (Canada) to the peninsula of Baja California, Mexico (Den Hartog, 1970; Phillips, 1979). Surfgrass species show partial depth segregation, with *P. torreyi* usually found deeper than *P. scouleri* and *P. serrulatus* (Phillips, 1979; Ramírez-García et al., 1998). This segregation is associated with the higher sensitivity of *P. torreyi* to air-exposure during low tide (Ramírez-García et al., 1998).

Although the distribution and community structure of surfgrass beds in the USA and Canada are relatively well known (Dudley, 1894; Littler and Murray, 1975; Phillips, 1979; Horn et al., 1983; Littler et al., 1983; Ricketts et al., 1985; Turner, 1985; Turner and Lucas, 1985; Stewart, 1989), the information available for the coasts of Baja California, Mexico is scarce (cf. Den Hartog, 1970; Phillips, 1979; Phillips and Meñez, 1988), and scattered through several herbarium collections in the USA and Mexico. Therefore, the actual distribution of the two species present in the Baja California peninsula, *P. torreyi* and *P. scouleri*, remains uncertain and the estimates of their abundance are very limited (Ramírez-García et al., 1998).

Surfgrass develops high-density stands which show levels of primary production above 8000 g DW m^{-2} y^{-1} (Ramírez-García et al., 1998), amongst the highest reported for seagrasses (Duarte and Chiscano, 1999). Presently it is unclear whether this high productivity is maintained due to high nutrient availability coupled to the high turbulence (Margalef, 1997) characteristic of the *Phyllospadix* habitat, or despite nutrient limitation: the nutrient status of these species is unclear.

The goals of the study were (1) to delimit the geographical distribution of the two species of surfgrass along the Pacific coasts of Baja California, Mexico, (2) to examine whether partial depth segregation between coexisting *P. torreyi* and *P. scouleri* is a general feature along the coast of Baja California, and (3) to explore experimentally whether the growth of these species could be limited by the availability of nutrients.

2. Methods

An extensive review of surfgrass specimens present at herbarium collections available at academic and research institutions in the USA and Mexico (Table 1) was conducted to derive the distribution of *Phyllospadix torreyi* and *Phyllospadix scouleri* along the coast of Baja California. We completed this information with three field surveys (March 1995, April 1996 and March 1998) along the western coast of the states of Baja California and Baja California Sur, as well as the eastern coast of Baja California Sur (southern sector of the Sea of Cortez). Details of locations in Baja California where surfgrass species have been found and of examined herbarium specimens may be downloaded from our website (http://www.ibiologia.unam.mx/directorio/ramirez-g.pdf).

Cover and depth distribution of intertidal *P. scouleri* and *P. torreyi* were estimated at three sites: in the north (Punta Campo López, Mesquitito), center (Punta Clambay, Bahía Tortugas) and south (Cerro El Vigía, Isla Santa Margarita) sectors of the Pacific coast of Baja California (Fig.1, Table 2). Transects (8 in Punta Campo López, 3 in Punta Clambay, and 3 in Cerro El Vigía) 40-50 m in length were haphazardly laid from the land to the seaward side of the intertidal and extending into the upper subtidal, and the percentage of substratum covered by *P. scouleri* and *P. torreyi* was estimated every 1 m along the transects using a 30 x 30 cm quadrat including a 10 x 10 cm grid. Transect depth (relative to a permanent marker) was recorded every 1 meter by laying a horizontal laser beam along the transects and measuring the vertical distance (± 1 cm) from it to the substratum. Transect measurements were made on 3-4 consecutive days at each site, and the distance between them was less than 50 m. All transect depths are reported relative to the mean lower low water level (MLLW), which was determined by marking the level of the sea at different times during a minimum of 3 complete tide cycles at each site and comparing them with the sea levels and times predicted by tide tables calculated for San Diego, California (http://www.co-ops.nos.noaa.gov/). Observed sea level varied from 0.26 m to 2.10 m in Punta Campo López, from 0.05 m to 2.33 m in Punta Clambay, and from –0.10 m to 2.18 m in Cerro El Vigía. The sea level during the maximum spring tides vary from –0.51 m to 2.19 m in the Pacific coast of Baja California.

The preliminary experimental evaluation of the nutrient-limited status of the growth of surfgrass was performed in Punta Clambay, Bahía Tortugas (Fig. 1) in March 1998. Two *P. scouleri* stands were selected in the lower intertidal and two *P. torreyi* stands were selected in the upper subtidal, 100 m apart from the *P. scouleri* stands. The distance between the two *P. scouleri* stands was 5 m while that between the two *P. torreyi* stands was 7 m. The size of the selected stands varied from 1 m^2 to 8 m^2. One of the stands selected for each species was haphazardly assigned to receive the addition of nutrients while the other served as control. Nutrients were added to the stands using 30 cm-long PVC cartridges with several holes perforated in their walls to allow the transit of seawater and the release of nutrients. Three cartridges, each containing 210 g of OSMOCOTE fertilizer (20N-10P-5K), were tied to the rocks (distance between each cartridge was 30 cm) at each of the nutrient-added surfgrass stands (nutrient load was about 126 g N, 63 g P and 31.5 g K per m^2). The cartridges were maintained at the sites for five days, after which 10-15% of the initial amount of fertilizer still remained inside. The *P. scouleri* stands were exposed to air during low tide for about six hours during day time each day of the experiment, whilst those of *P. torreyi* always remained submersed.

Two 10 x 10 cm quadrats were delimited at each of the nutrient-added and control surfgrass stands. Inside each of the quadrats 10 shoots were marked with a small cable tie and two collinear holes were punched just below the ligule of the oldest leaf of each shoot to estimate leaf growth. All surfgrass biomass present in the quadrats was collected after 5 days, washed with seawater and freshwater, sorted into rhizomes plus roots and leaves, and dried at 70 ºC for 48 hours. Prior to that the number of leaves, the length and width of the shoot, and the number of new leaves and new portions of the blades grown during the marking period were measured in the marked shoots (number of recovered marked shoots varied from 5 to 10 depending on the quadrat). Dried leaves and rhizome plus roots from nutrient-added and control quadrats were pooled and ground with a mortar and pestle. Three aliquots of each nutrient-added and control plant material were analyzed to determine total nitrogen and phosphorus. Surfgrass samples were digested with 10 ml of concentrated sulfuric acid and 5 ml of 35 % hydrogen peroxide at 450 ºC during one hour, and brought to a final volume of 75 ml with distilled water. A subsample of 5 ml was analyzed for total phosphorus (Murphy and Riley, 1962). The remaining product of the digestion was analyzed for total nitrogen (Kjeldahl, 1883; TECATOR, 1979; 1987).

Due to lack of replication in the treatments at the species level the differences in nutrient content, shoot length, shoot biomass and leaf growth between nutrient-added and control stands can not be evaluated using statistical tests and, therefore, only means and standard errors of all the shoots collected at the end of the experiment in each stand are presented.

3. Results

3.1. Distribution and depth segregation along the coast of Baja California

Surfgrass was present along the Pacific coast of Baja California from Isla Coronado (32° 23’ N, 117° 14’ W) in the north to Isla Santa Margarita (24° 31’ N, 111° 59’ W) in the south (Fig. 1, Table 2), and both species (*Phyllospadix torreyi* and *Phyllospadix scouleri*) had the same range (Fig. 1, Table 2).

Although *Phyllospadix scouleri* was collected by I.L. Wiggins (5566, 30/04/1931; DS, POM) at Punta Conejo (Baja California Sur, 24° 04’ N 111° 01’ W), we could not find living plants anchored to the substratum during our visits to the site. We did find beach cast material of *Phyllospadix* and *Zostera,* but cannot exclude that currents transported them there. Local reports of *Phyllospadix* collections in the beaches of Bahía de La Paz (Baja California Sur) likely have a similar origin.

Transect measurements show that *Phyllospadix scouleri* is distributed higher in the lower intertidal and upper subtidal than *Phyllospadix torreyi* (Fig. 2). The cover of *P. torreyi* generally increased from the lower intertidal towards the subtidal, whilst that of *P. scouleri* reached a maximum and decreased towards the subtidal.

3.2 Preliminary evaluation of nutrient enrichment

The content of nitrogen and phosphorus in the leaves of *Phyllospadix scouleri* was high, and was similar in the control and the nutrient-added stand (Table 3). The nitrogen content of the leaves of *Phyllospadix torreyi* was also similar in the control and nutrient-added stand, whilst phosphorus content had increased by 13% in the nutrient-added stand (Table 3). The atomic N/P ratio in the leaves of *P. scouleri* was 7.8 both in the control and nutrient-added stand, while it was 8.0 in the control stand and 7.6 in the nutrient-added stand of *P. torreyi*.

Shoot length and biomass were very similar in the control and the nutrient-added stand of *Phyllospadix scouleri*, but were 25 % and 49 % larger in the nutrient-added than in the control stand of *Phyllospadix torreyi* (Table 3). Similarly, leaf growth rates of *P. scouleri* appeared unaffected by nutrient addition, but those of *P. torreyi* were almost twice as high compared to the controls. Leaf turnover (growth rate/ shoot biomass at marking time) was not affected in either species(Table 3).

Discussion

Surfgrass was found to be present along the Pacific coast of the Baja California peninsula from Isla Coronado in the north to Isla Santa Margarita in the south, and both species (*Phyllospadix torreyi* and *Phyllospadix scouleri*) had the same latitudinal range. Furthermore, no rooted surfgrass material has been found south of 24º 20’ N, which corresponds to the southern end of Isla Santa Margarita, and on the eastern coast of Baja California Sur (southern sector of the Sea of Cortez, Fig. 1). South of Isla Santa Margarita the Pacific coast of Baja California peninsula is formed mainly by marine clastic and alluvial coastal deposits (Atlas Nacional de Mexico, 1990), which are unsuitable for surfgrass establishment. The few rocky substrata present in this part of the coast (Punta Lobos, 23º 25' N, and further south, Cabo San Lucas) did not hold any surfgrass population, which suggests that the southern limit of surfgrass distribution in Baja California is not limited by the availability of suitable substratum.

Previous reports of surfgrass in the southernmost part of Baja California coast, on the Pacific side (Wiggins, 1980) and in the Sea of Cortez (beaches of Bahía de La Paz: Riosmena-Rodríguez and Sánchez-Lizaso, 1996), might derive from surfgrass fragments transported there by marine currents rather than observations of rooted stands. There is indeed no evidence that surfgrass can grow on sandy substrata as suggested by Riosmena-Rodríguez and Sánchez-Lizaso (1996). Furthermore the absence of surfgrass inside the Sea of Cortez is corroborated by previous surveys of the coast and islands (Ramírez-García and Lot, 1994).

The comparison of the presence of surfgrass along the Pacific coast of Baja California with the distribution of surface sea water temperatures in winter and summer shows that surfgrass is absent from sites where the sea surface temperature exceeds 21 ºC in winter and 27 ºC in summer, which suggests that either one of these water temperatures or both could determine the ability of surfgrass to thrive. There is indeed evidence of a low tolerance to higher temperature by *Phyllospadix*, since an experimental increase of water temperature from 13 ºC (the typical winter surface value at Central California coast) to 21 ºC resulted in a 60% reduction in *Phyllospadix torreyi* leaf growth rates (Drysdale and Barbour, 1975). The importance of seawater temperature in determining the southern limit of surfgrass distribution in Baja California is further supported by the loss of surfgrass and *Macrocystis* populations in Bahía Tortugas (Baja California Sur) after the 1997-98 El Niño event (Ramírez-García, pers. obs.), which further suggests that surfgrass populations in Baja California Sur might be impacted by the temperature increase predicted by current global change models.

Our observations confirm that *Phyllospadix scouleri* is distributed higher in the lower intertidal and upper subtidal than *P. torreyi* along the coast of Baja California, which is consistent with previous descriptions for the Pacific coast of North America (Phillips 1979). *P. torreyi* is more sensitive to desiccation than *P. scouleri*, which explains why the latter species is able to grow at shallower depths than the former (Ramírez-García et al., 1998). Our results also show that *P. torreyi* is more abundant than *P. scouleri* in the upper subtidal, which suggests that *P. torreyi* is a more successful competitor for habitat space than *P. scouleri* when the stress associated to desiccation during low tides disappears.

The nitrogen and phosphorus content of the leaves of both species of surfgrass was well above the median values for seagrasses (1.8 % N and 0.2 % P as % of DW, cf. Duarte, 1990), suggesting an adequate nutrient supply in their habitat. The atomic N/P ratio of surfgrass leaves was one third of the median N/P ratio for seagrasses (24, cf. Duarte 1990), which indicates that surfgrass leaves are comparatively enriched in phosphorus, and suggests that the availability of phosphorus might be higher than that of nitrogen. Although the lack of replication of the nutrient-addition experiment prevents the use of statistical tests to evaluate the differences between treatments and species, the overall picture from the results is that *Phyllospadix torreyi* was more responsive to the addition of nutrients than *P. scouleri*. This preliminary experiment suggests that *P. torreyi* might have higher nutrient requirements or experience lower nutrient availability than *P. scouleri*.

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Table 1. Academic and research institutions whose herbaria were visited to examine surfgrass specimens and identify their collection sites.

Acronym	Institution
AHFH	Herbarium of Allan Hancock Foundation, University of Southern California, USA.
ARIZ	Herbarium of University of Arizona, USA.
CAS	Department of Botany, Academy of Sciences, San Francisco, California, USA
DS	Dudley Herbarium of Stanford University, Academy of Sciences, San Francisco, California, USA.
LAM	Los Angeles County Museum of Natural History, California, USA.
MEXU	Herbario Nacional de México, Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, México DF.
POM	Herbarium of Pomona College, Rancho Santa Ana Botanic Garden, California, USA.
RSA	Herbarium, Department of Botany, Claremont, California, USA.
SD	San Diego Museum of Natural History, San Diego, California, USA.
UC	Herbarium of Department of Botany, University of Berkeley, California, USA.

Table 2. Locations along the Pacific coast of Baja California peninsula (México) where surfgrass is present based on the information obtained from the examination of herbarium collections (cf. Table 1) and our own field survey (see Methods). State: B.C., Baja California; B.C.S., Baja California Sur. Source: H, herbarium collection; F, field survey (specimens deposited at MEXU herbarium); T, transect study.

Location	State	Latitude, Longitude	*Pyllospadix scouleri*	*Phyllospadix torreyi*	Source
1. Isla Coronado	B.C.	N 32º 23’ W 117º 14’	X		H
		N 32º 25’ W 117º 15’	X		H
2. Punta Descanso	B.C.	N 32º 16’ W 117º 01’		X	H
3. Punta Campo López (Mesquitito)	B.C.	N 32º 10’ W 116º 55’	X	X	F, T
4. El Mirador	B.C	N 31º 54’ W 116º 39’		X	F
5. Bahía Ensendada Todos Santos	B.C.	N 31º 51’ W 116º 46’		X	H
		N 31º 05’ W 116º 46’		X	H
6. Punta Morro	B.C.	N 31º 52’ W 116º 40’	X		F
7. Punta Banda	B.C.	N 31º 45’ W 116º 45’	X		H
8. Isla San Martín	B.C.	N 30º 28’ W 116º 06’	X		H
9. Isla San Jerónimo	B.C.	N 29º 45’ W 115º 47’	X		H
		N 29° 45’ W 115° 47’		X	H
10. Punta San Carlos	B.C.	N 29º 37’ W 115º 29’	X		H
11. Isla Guadalupe	B.C.	N 29º 10’ W 118º 16’		X	H
		N 29º 09’ W 118º 16’		X	H
		N 29º 00’ W 118º 25’		X	H
		N 28º 58’ W 118º 18’		X	H
12. Isla Cedros	B.C.S.	N 28º 17’ W 115º 15’	X		H
		N 28º 00’ W 115º 14’		X	H
		N 28º 08’ W 115º 20’	X		H
13. Isla San Benito	B.C.S.	N 28º 18’ W 115º 35’	X		H
		N 28º 16’ W 115º 21’	X		H
		N 28º 18’ W 115º 34’	X		H
		N 28º 18’ W 115º 33’		X	H
14. Isla Natividad	B.C.S.	N 27º 51' W115º 10'	X		F
		N 27º 54' W115º 15'		X	H
15. Bahía Sebastián Vizcaíno	B.C.S.	N 27º 52’ W 115º 02’	X		H
		N 28º 14’ W 114º 06’	X	X	F
		N 27º 45’ W 114º 50’		X	F
16. Bahía Tortugas (Punta Clambay)	B.C.S.	N 27º 39’ W 114º 52’		X	F, T
		N 27º 36’ W 114º 51’	X	X	F, T
17. Bahía La Asunción	B.C.S.	N 27º 09' W 114º 15'	X		H
18. Isla La Asunción	B.C.S.	N 27º 06' W 114º 16'	X		H
		N 27º 06' W 114º 18'	X		H
19. Isla San Roque	B.C.S.	N 27º 07' W 114º 23'	X		H
20. Estero El Coyote	B.C.S	N 26º 50' W 113º 33'	X		H
21. Punta Abreojos	B.C.S.	N 26º 43' W 113º 35'	X		H
22. Bahía San Juanico	B.C.S.	N 26º 20' W 112º 30'	X		H
23. Arroyo San Gregorio	B.C.S.	N 26º 03' W 112º 17'	X		H
24. Isla Magdalena	B.C.S.	N 24º 45' W 112º 24'	X		H
		N 24º 32' W 112º 05'	X		
25. Isla Santa Margarita (Cerro El Vigía)	B.C.S	N 24º 31', W 111º 59'	X	X	F, T

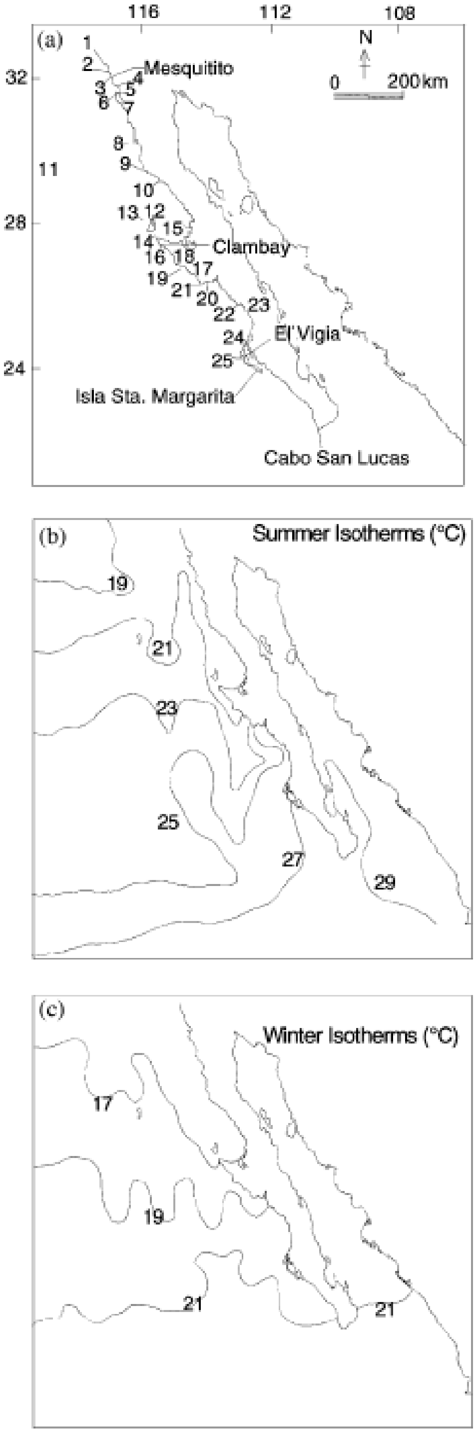
Table 3 Shoot biomass and length, leaf growth, and nitrogen and phosphorus content in leaves of surfgrass for the preliminary nutrient addition experiment in Punta Clambay, Bahía Tortugas, Baja California, Mexico (see Fig. 1) in nutrient-added and control stands in March 1998.

Variable	*Phyllospadix scouleri*		*Phyllospadix torreyi*	
	Control Mean ± SE (n)	Nutrient-added Mean ± SE (n)	Control Mean ± SE (n)	Nutrient-added Mean ± SE (n)
Shoot biomass, mg DW shoot^{-1}	108 ± 12 (11)	114 ± 13 (14)	108 ± 10 (15)	163 ± 18 (17)
Shoot length, cm shoot^{-1}	32 ± 2 (11)	29 ± 2 (14)	53 ± 3 (15)	66 ± 5 (17)
Leaf growth, cm shoot^{-1} d^{-1}	0.9 ± 0.15 (11)	1.3 ± 0.2 (14)	1.4 ± 0.24 (15)	2.4 ± 0.32 (17)
Leaf growth, mg DW shoot^{-1} d^{-1}	0.6 ± 0.1 (11)	1.1 ± 0.23 (14)	0.8 ± 0.14 (15)	1.7 ± 0.3 (17)
Leaf turnover, d^{-1}	0.007 ± 0.001 (11)	0.009 ± 0.001 (14)	0.009 ± 0.002 (15)	0.011 ± 0.001 (17)
Leaf nitrogen, % DW	2.3 ± 0.22 (3)	2.4 ± 0.26 (3)	2.2 ± 0.03 (3)	2.4 ± 0.07 (3)
Leaf phosphorus, % DW	0.7 ± 0.02 (3)	0.7 ± 0.01 (3)	0.6 ± 0.01 (3)	0.7 ± 0.01 (3)

Figure captions

Fig. 1. Locations (cf. Table 2) along the Pacific coast of Baja California peninsula (México) where surfgrass presence has been reported (a), and isotherms of surface seawater temperature in summer (b) and winter (c).

Fig. 2. Mean percent cover of surfgrass species in the intertidal and subtidal of three sites in the (a) north (Punta Campo López, Mesquitito), (b) center (Punta Clambay, Bahía Tortugas), and (c) south (Cerro el Vigía, Isla Santa Margarita) sectors of the Pacific coast of Baja California (México). Depth is shown relative to MLLW sea level. Error bars represent ± 1 standard error.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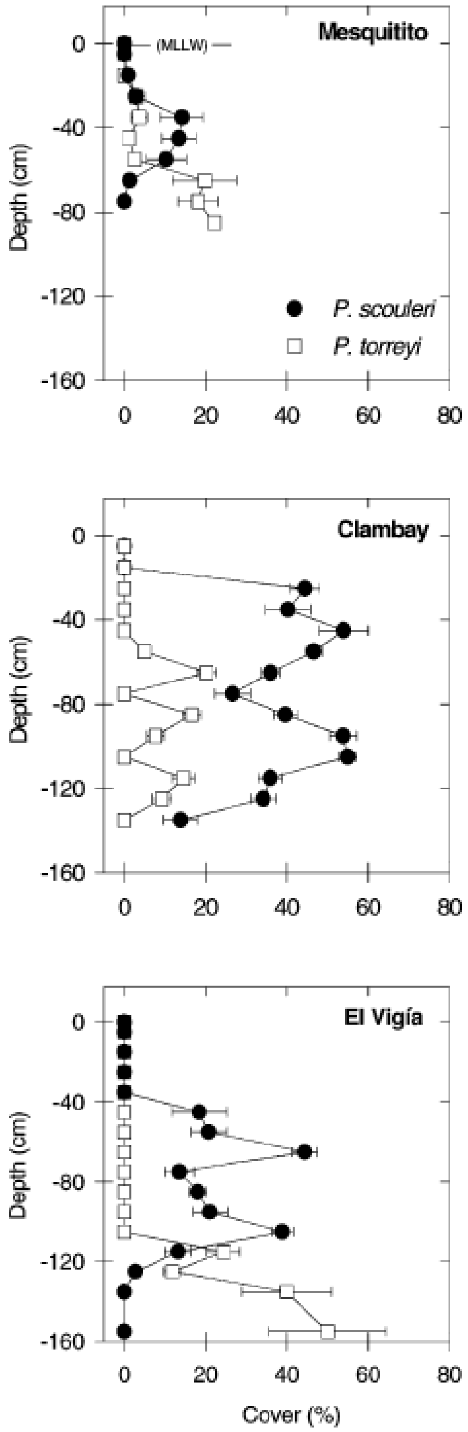
24
(a)
Mesquitito
Clambay
El'Vigia
Isla Sta. Margarita
Cabo San Lucas
N
0
200 km
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
(b)
Summer Isotherms (°C)
19
21
23
25
27
29
(c)
Winter Isotherms (°C)
17
19
21
21


Mesquitito
(MLLW)
Depth (cm)
0
-40
-80
-120
-160
0
20
40
60
80
P. scouleri
P. torreyi
Clambay
Depth (cm)
0
-40
-80
-120
-160
0
20
40
60
80
El Vigía
Depth (cm)
0
-40
-80
-120
-160
0
20
40
60
80
Cover (%)

1